Environmental Biology of Fishes **55**: 99–114, 1999.

The ecology, behavior, and conservation of the tidewater goby, *Eucyclogobius newberryi*

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Received 5 January 1997   Accepted 24 December 1997

Key words: Gobiidae, endangered species, extinction, fisheries management, reproduction, lagoon, estuary, California

Synopsis

Understanding the ecology and behavior of endangered species, such as the tidewater goby, *Eucyclogobius newberryi,* is important for identifying problems and formulating solutions for species recovery. The tidewater goby forms isolated populations in California's coastal lagoons, creeks, and marshes. Rapid declines in the number of populations led to its listing as an endangered species in 1994. This benthic fish prefers stillwater habitats and feeds on small invertebrates. It is an annual species with an extended breeding season. Fish are larger in marsh habitats than in lagoon or creek habitats. The male digs a spawning burrow, preferably in sand, where he provides care for a single clutch. The tidewater goby is sex-role reversed: females compete more intensely than males for access to mates. The tidewater goby is a species at risk, in part due to narrow habitat preferences, isolation of populations, short lifespan, lack of marine dispersal, and vulnerability to introduced predatory fishes. Attributes that favor its recovery include euryhaline tolerances, rapid reproductive rate, its potential for opportunistic feeding, and the possibility of natural recolonization under certain circumstances. Potential conservation measures include protecting coastal marshes that adjoin creeks and lagoons, maintaining natural hydrologic regimes, preventing artificial breaching of the sandbar at the estuary's mouth, and preventing introductions of predatory fishes. Captive breeding and reintroduction of tidewater gobies are potential tools for recovery, provided that underlying problems of habitat availability and suitability and issues of genetic integrity and disease transmission are addressed. Further research into the tidewater goby's utilization of marsh habitats, dispersal mechanisms, response to artificial breaching events, and metapopulation genetics would provide additional information for management.

Introduction

The plight of small fishes is often overlooked by the public and even by conservation biologists (Allendorf 1988, Sheldon 1988, Maitland 1995) when compared to the problems of readily visible 'charismatic megafauna', such as whales and whooping cranes, or fishes important for commercial or sport fisheries, such as salmonids and centrarchids. Small fishes are often perceived simply as 'minnows', valuable only as bait or as food for game fish (Sheldon 1988, Warren & Burr 1994). Yet conservation of these fishes is valuable for a variety of scientific, economic, public health, aesthetic, and ethical reasons (Ono et al. 1983, Pister 1985, Moyle & Williams 1990, Bruton 1995, Moyle & Moyle 1995).

The most imperiled freshwater fish fauna in the United States is in the arid west (Moyle & Williams 1990, Warren & Burr 1994). Declines of native freshwater fishes stem from aggressive human exploitation of scarce water resources (Minckley & Deacon 1968, 1991, Reisner 1986), coupled with introductions of warmwater fishes (e.g. centrarchids) better suited to altered habitats (Moyle & Williams 1990, Moyle 1995). While desert fishes such as cyprinodontids are the most prominent example of endangered fishes in California (e.g., Minckley & Deacon 1968, 1991), coastal freshwater and estuarine fishes are also threatened, especially in the south coastal region (Moyle & Williams 1990, Swift et al. 1993, Moyle 1995).

The tidewater goby, *Eucyclogobius newberryi*, is a small benthic fish, endemic to California's coastal lagoons, creeks, and marshes (Moyle 1976, Swift et al. 1989). It is an annual species that rarely exceeds 50 mm standard length (SL). Tidewater goby populations have declined, especially in southern California and San Francisco Bay (Swift et al. 1989, 1993, Lafferty et al. 1996). An apparent rangewide decline of 35 percent over six years (1984–1990) prompted the U.S. Fish and Wildlife Service to list it as an endangered species in 1994 (U.S. Fish & Wildlife Service[1]).

This species is threatened by habitat loss and degradation (e.g., development of coastal wetlands and waterways, water diversions, and stream channelization), and, to a lesser degree, predation by exotic fishes (USFWS[1], Lafferty et al. 1996).

The sexual behavior of the tidewater goby is unusual (Swenson 1997). In many ways the tidewater goby is a typical gobiid, with its epibenthic lifestyle and male parental care of eggs in a burrow. But closer examination reveals some unusual reproductive behavior: females compete more intensely than males for access to potential mates and display more striking breeding coloration than males (Swift et al. 1989, Swenson 1997). This sex-role reversed mating pattern is rare among animals (Clutton-Brock & Vincent 1991, Vincent 1992). Study of such 'exceptions to the rule' (Williams 1975) provides an opportunity to test theories of sexual selection.

Study of the tidewater goby is therefore important for both conservation biology and behavioral ecology. Management and conservation efforts will depend on an understanding of the natural history of this endangered species (e.g., Simberloff 1988, Greene 1994, Tear et al. 1995). Furthermore, understanding its unusual mating behavior will advance sexual selection theory by investigating the mechanisms responsible for intrasexual competition, such as differences between the sexes in potential reproductive rates (e.g., Clutton-Brock & Vincent 1991). In this paper I review the ecology and behavior of the tidewater goby, using my studies of two populations in north-central California and other studies to illustrate key points. I discuss the traits that place the tidewater goby at risk, its prospects for recovery, and the management applications of behavioral studies in general.

Study site

As a consequence of climate and coastal geography, California estuarine systems differ greatly from those on the western Atlantic coast. California's climate is Mediterranean, with wet winters and dry summers. During the summer drought, streamflow decreases and ocean waves deposit sand on the beach. In many coastal streams this results in a sandbar that closes the mouth to form a lagoon (Smith[2,3], Josselyn et al. 1991, Ferren et al.[4]). After

[1] U.S. Fish & Wildlife Service (USFWS). 1994. Endangered and threatened wildlife and plants: determination of endangered status for the tidewater goby. 4 February 1994, Federal Register 59 (24): 5494–5499.

[2] Smith, J.J. 1987. Aquatic habitat and fish utilization of Pescadero, San Gregorio, Waddell and Pomponio Creek estuary/lagoon systems. California Department of Parks and Recreation, Interagency Agreement 4-823-6004 with the Trustees for California State University. 30 pp.

[3] Smith, J.J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pomponio Creek estuary/lagoon systems, 1985–1989. California Department of Parks and Recreation, Interagency Agreement 84-04-324 with the Trustees for California State University.

[4] Ferren, Jr., W.J., P.L. Fiedler & R.A. Leidy. 1995. Wetlands of the central and southern California coast and coastal watersheds: a methodology for their classification and description. 6 February 1995. Report to the U.S. Environmental Protection Agency. Environmental Report No. 1, Museum of Systematics and Ecology, Department of Biological Sciences, University of California at Santa Barbara.

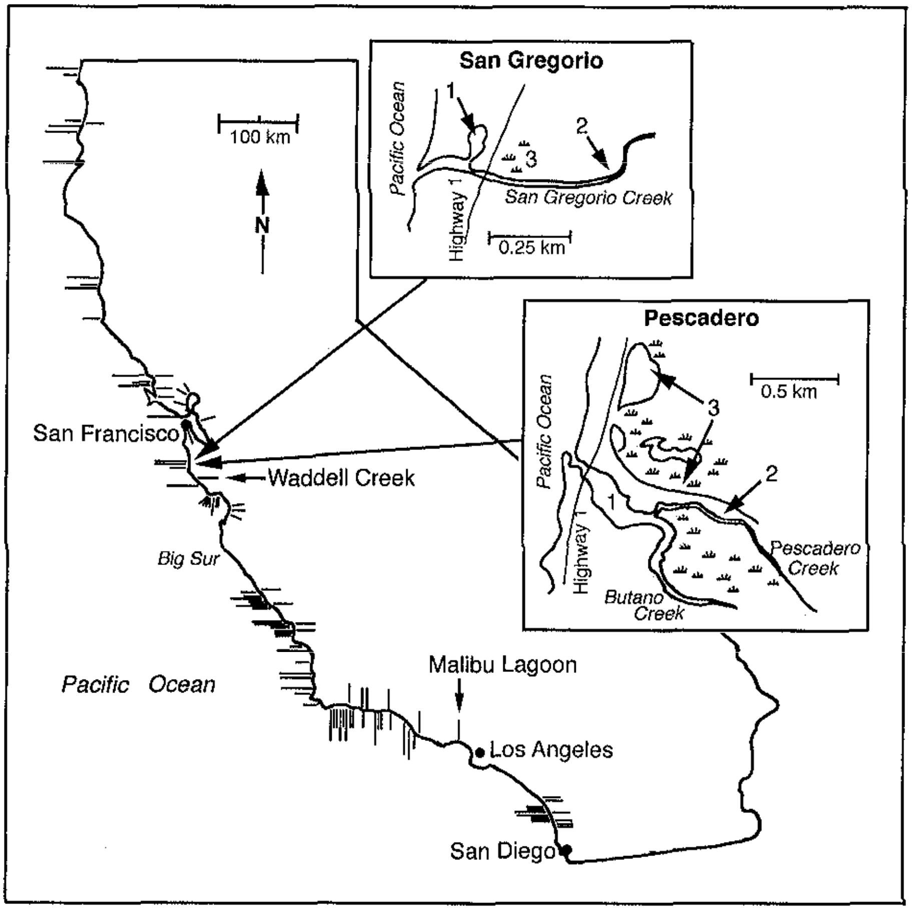

Figure 1. Distribution of the tidewater goby in California in 1995 (adapted from Swift et al. 1989 and Swift unpublished data) and location of study sites. Long lines to left (offshore) = large populations, and localized or small populations in large, relatively stable habitat. Short lines to left (offshore) = intermittent populations that are sometimes rare or extirpated, and populations with uncertain status due to small size or extensive impact on the habitat. Lines to right (inland) = extirpated locality (fish reintroduced to Wadell and Malibu in 1991). In cases of close overlap, not all localities are plotted. The inset maps indicate the location of sampling sites at San Gregorio Creek and Pescadero Creek, San Mateo County: (1) lagoon site, (2) creek site, and (3) marsh site(s). Lagoons fluctuated greatly in size, depending on closure of the creek mouth and tidal inundation.

closure to tidal exchange, the estuary is diluted by freshwater inflow. The sandbar is normally breached around November or December with the onset of winter rains. A similar pattern of seasonal closure occurs in the estuaries of southwestern Australia and southeastern Africa, although these estuaries are usually much larger and frequently become hypersaline (reviewed by Day 1981, Potter et al. 1990). The topography of California's coastline is steep, due to three mountain ranges that extend along the coast and to coastal terraces formed by wave action and uplift of the land relative to sea level (Ferren et al.[4]). Unlike Atlantic coast estuaries, many small California estuaries are formed at the mouths of steep canyons and lack extensive intertidal floodplains.

I studied two populations of tidewater gobies in north-central California. San Gregorio Creek and Pescadero Creek are small coastal streams located approximately 50 km south of San Francisco and 6 km apart (Figure 1). Tidewater gobies inhabited the three contiguous major habitats found in both streams: lagoon, creek, and marsh.

The lagoon was the habitat closest to and contiguous with the Pacific Ocean. Its substrate was predominantly sand. Lagoon habitats fluctuated in depth (usually 0.3–1.5 m) and areal extent depending on the water's surface elevation, which is a function of tides, freshwater inflow, and the elevation of the sandbar at the mouth. Lagoons are considered the most typical habitat of the tidewater goby (Swift et al. 1989).

Brackish marsh habitats in California can be partially or completely isolated hydrologically from the nearby lagoon or creek. Water exchange between the marsh and creek was partial at San Gregorio and minimal at Pescadero. Water levels did not fluctuate much with the tidal regime. The marsh at San Gregorio occasionally dried during the summer, while the marsh at Pescadero was more extensive and remained wet year-round. Marsh habitats had a soft mud and silt substrate and were fringed by emergent vegetation such as pickleweed *Salicornia virginica*, bulrush *Scirpus robustus*, and saltgrass *Distichlis spicata*.

The creek upstream of the lagoon was influenced by tides, depending on outflow. The substrate was mud and/or gravel and mud, with occasional patches of silty sand. During the summer the currents were sluggish when the mouth was closed and flow was diminished.

The waters of the lagoon and lower creek were often vertically stratified in both salinity and temperature when the mouth was open. The bottom was saltier and often warmer than the surface. This stratification was absent in the marsh habitats, which were buffered from tidal inputs and were usually shallower. Submerged vascular plants (*Ruppia* or *Potamogeton*) grew in all three habitats and were especially dense in late summer.

Human disturbance in the area included agriculture, breaching of sandbars to open stream mouths, bridge and highway construction, and siltation (Viollis 1979). Portions of the marsh at San Gregorio and Pescadero were historically drained and farmed. Although these particular fields were later abandoned, farming continues today in both watersheds. Such activities affect the downstream habitats through water diversions for irrigation, use of fertilizer and pesticides, and erosion. In the past, local residents artificially breached the sandbar that blocks the mouth of Pescadero Creek. This was done out of concern for upstream flooding and to allow passage of anadromous steelhead, *Oncorhynchus mykiss*, during spawning migrations (J. Smith personal communication). Such practices have been discouraged in recent years to avoid disturbing the aquatic resources of these small estuaries during the late summer and fall.

Construction of highway bridges has also affected geomorphology and hydrology. At San Gregorio the marsh and lagoon were partially filled during Highway 1 construction and the creek was directed to a more southerly channel under the bridge. The marsh is now connected to the creek only by a small culvert. Over time the creek bed elevation has dropped, resulting in the draining of the marsh when water levels in San Gregorio Creek are low.

Finally, accelerated erosion from agriculture and logging has resulted in increased sedimentation in Pescadero Marsh and lagoon (Viollis 1979). For example, in the 1980's the bottom of Pescadero lagoon was sometimes covered with a 10–15 cm layer of silt. Thus, although the lower reaches of both San Gregorio Creek and Pescadero Creek have been protected as state parks for the last few decades, historic and current human disturbances in the watershed continue to influence these ecosystems.

Review of ecology and behavior

Distribution and status

Swift et al. (1989) surveyed streams and museum collections to determine the past and current distribution of tidewater gobies in California. Tidewater gobies have been historically documented at 87 localities ranging from Tillas Slough (mouth of Smith River), Del Norte County near the northern border with Oregon, to Agua Hedionda Lagoon at Carlsbad, San Diego County, approximately 48 km north of San Diego (Figure 1). Regions with a steep coastline where lagoons do not form, such as the Big Sur coast between Monterey Bay and Arroyo del Oso, do not harbor the species, resulting in a discontinuous distribution pattern (Swift et al. 1989). Localities that support tidewater goby are typically coastal lagoons that form at the mouths of streams or seasonally wet canyons, or the upper edge of tidal bays such as Morro Bay, San Luis Obispo County (C. Swift personal communication).

In 1984 the number of known populations of tidewater gobies was 63 (Swift et al. 1989). By 1991 twenty four populations had disappeared and five small populations were rediscovered, suggesting a rangewide decline of 35 percent in six years (USFWS[1]). C.C. Swift petitioned the U.S. Fish and Wildlife Service in 1990 to list the tidewater goby under the federal Endangered Species Act. At that time, most of the 43 remaining populations were small and apparently threatened by a variety of human and natural factors. California was experiencing an extended drought (1987–1992). According to Swift's petition, only eight extant populations were large enough and safe enough from habitat degradation to be considered secure for the immediate future (USFWS[1]) These areas were all north of San Francisco Bay. In 1994 the tidewater goby was listed as an endangered species. In 1996, about 55–60 populations were estimated in California (E. Ballard personal communication). This increase could be due to increased sampling efforts in recent years, population growth following the drought in streams where gobies had been rare or overlooked, and possible recolonization of extirpated populations.

Most of California's human population is concentrated along the coast, with approximately half located in the southern third of the state, between Santa Barbara and San Diego. Tidewater gobies are consequently most threatened in Southern California. Habitat loss and alteration can be attributed to destruction of coastal wetlands for urban development and agriculture, stream channelization, flood control projects, stream dewatering via groundwater pumping or upstream diversions, effluent from wastewater treatment plants, artificial breaching of creek mouths, highway widening and bridge projects, and cattle grazing (Swift et al. 1989, Moyle & Williams 1990, Josselyn et al. 1991, Nordby & Zedler 1991, Swift et al. 1993, Brown & Swenson 1994, Capelli 1997).

Habitat preferences

Tidewater gobies can occur in a variety of estuarine habitats. In San Gregorio and Pescadero creeks, tidewater gobies inhabited sandy lagoons, mud- or mud-and-gravel-bottomed reaches of creeks, and muddy marsh pools and channels, although they were not present in all habitats every month (Swenson 1995).

Although tidewater gobies can tolerate a wide range of salinities, they appear to prefer low-salinity water (0–10 ppt), an unusual trait among Pacific coast fishes (Swift et al. 1989). Tidewater gobies have been found in wide ranges of salinity (0–30 ppt) and temperature (9–25°C) (Swift et al. 1980, Worcester 1992, Swenson 1995). In laboratory experiments they tolerated salinities up to 41 ppt (Swift et al. 1989). Few fish species are as restricted to the coastal lagoon habitat as is the tidewater goby (Swift et al. 1993), although many species may extend into brackish water from either marine (e. g. arrow goby *Clevelandia ios* and staghorn sculpin *Leptocottus armatus*) or freshwater habitats (e. g. tule perch *Hysterocarpus traski* and splittail *Pogonichthys microlepidotus*), or may migrate through estuaries (e. g. steelhead *Oncorhynchus mykiss*) (Moyle 1976). Most gobies in California are found in more marine habitats, such as the arrow goby and bay goby *Lepidogobius lepidus* in bays and mudflats (Brothers 1975), and the bluebanded goby *Lythrypnus dalli* in rocky marine habitats (Wiley 1976). Conversion of many coastal lagoons to harbors by artificially maintaining an open entrance has altered salinity and temperature regimes and produced conditions more akin to bays and the ocean, which do not favor the species (Swift et al. 1993). Tidewater gobies have been documented as far as 8 km upstream of lagoon habitat in two southern California populations: San Antonio Creek in a beaver pond (Irwin & Soltz[5]) and the Santa Ynez River (C. Swift personal communication).

Tidewater gobies are intolerant of all but slow currents (Swenson 1995). In my studies gobies were rarely collected from flowing waters or areas with

[5] Irwin, J.F. & D.L. Soltz. 1984. The natural history of the tidewater goby, *Eucyclogobius newberryi*, in the San Antonio and Schuman Creek system, Santa Barbara County, California. U.S. Fish and Wildlife Service, Sacramento Endangered Species Office Contract No. 11310–0215–2. 33 pp.

strong wave wash and they appeared to avoid these conditions, which occurred in the creek habitat during winter when rainfall elevated stream discharge. For example, during sampling on 23 February 1992 in the creek at Pescadero, gobies were absent from the main channel, which was flowing at 0.15 m s^{-1} (surface velocity), but were densely concentrated in an adjacent backwater pool. Observations of captive gobies suggested that they are weak swimmers, although they can use their fused pelvic fins as a sucker to hold on to the substrate.

The availability of slack-water refuges, such as marshes and backwater areas of lagoons, may be critical during the winter rainy season, when flows in the creek increase dramatically. Jack Nelson has suggested that the heavy flows in the winter of 1972–1973 eliminated the population at Wadell Creek, Santa Cruz County (C. Swift personal communication). Access to stillwater refuges can be affected by water diversion, artificial breaching of the mouth, and other factors that reduce water elevations in the system prior to the winter floods. If the marsh is dewatered, fish cannot access this refuge and are concentrated in the main channel. The risk of flushing gobies out of stream systems has probably increased in recent times, as development of coastal wetlands, stream channelization, and flood control projects eliminate backwater habitat and increase flood peaks.

Tidewater gobies in San Gregorio and Pescadero were usually found in shallow water (< 1 m deep) close to shore (Swenson 1995). Many localities in California have little or no habitat deeper than this (Swift et al. 1989). Tidewater gobies occurred both over unvegetated substrate and in areas with submerged vegetation. Worcester (1992) found that adults were more abundant in sparse to moderate amounts of submerged vegetation, while larvae were more abundant in open, deeper (70 cm) water.

Previous research has focused on coastal lagoons (e.g., Swift et al. 1989, Worcester 1992), but marshes are also important habitats (Swenson 1995). Tidewater gobies attained significantly larger sizes in marsh habitats than in lagoon or creek habitats (Swenson 1995, Swenson & McCray 1996). It may be that the more stable physical conditions of the marsh foster improved growth or a more consistent or abundant supply of prey (Swenson & McCray 1996). Marshes can also be important refuges (e.g., Sedell et al. 1990) and could provide a source for naturally restocking the creek or lagoon. Efforts to designate critical habitat for recovery plans should consider the availability of marsh habitat, in addition to the more traditional lagoon habitat.

Abundance

Gobiids are frequently among the most abundant fishes in estuaries (Grossman et al. 1980, Day 1981, Potter et al. 1993, Gill et al. 1996). Tidewater gobies can be locally abundant, often outnumbering other fishes in certain localities. Their distribution, however, can be variable both spatially and seasonally. Patchy distribution within habitats has been documented using meter-square drop traps for fine-scale sampling. Density (gobies per square meter) ranges at Little Pico Creek, San Luis Obispo County were 0–67 in May 1990 (mean ± SD = 20.0 ± 19.0, n = 30 trap samples), 0–138 in November 1990 (10.0 ± 30.2, n = 30), and 0–27 in February 1991 (2.9 ± 5.0, n = 30) (Worcester 1992). Density ranges in other populations in October 1992 included 10–25 gobies per square meter (mean ± SD = 18.2 ± 5.1, n = 8) in the San Gregorio lagoon (1992), 3–75 (32.5 ± 33.2, n = 4) in the creek at San Gregorio (1992), 0–198 (45.8 ± 85.6, n = 5) in Pescadero marsh (1992) (Swenson 1995), and 0–91 (15.2 ± 24.7, n = 34) in Rodeo Lagoon, Marin County (1995) (Swenson & Taylor unpublished data). Efforts to estimate density using seine nets over larger areas have yielded slightly less variable results. In Rodeo Lagoon during October, the range of densities was 0–14.2 gobies per square meter (1.8 ± 4.0, n = 15).

This spatial variability can complicate estimation of population size. Attempts at estimates have ranged from fewer than 100 fish in small lagoons that measure 10–30 m long and a few meters wide (Swift et al. 1989) to a few hundred thousand in the San Gregorio system (Swenson 1995) and perhaps a few million in Lake Earl, a large (1100 ha) estuary in Del Norte County (Swift et al. 1989). Abundance can fluctuate seasonally and annually, as suggested by seine samples at Aliso Creek Lagoon, an average-

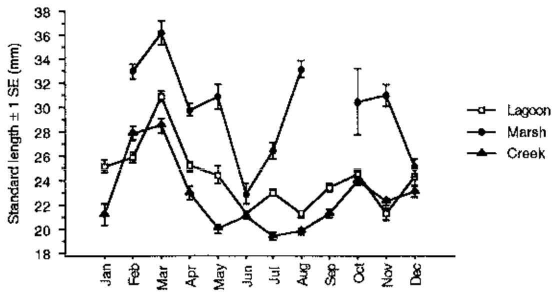

Figure 2. Annual pattern of mean body size (standard length ± 1 SE) of tidewater gobies collected from three habitats (lagoon, creek, and marsh) in San Gregorio Creek. These means represent data pooled from August 1991 to July 1993. Data from Swenson (1993, 1995).

sized lagoon (350–450 m long and 10–20 m wide) in southern California. Population estimates ranged from 1000–1500 gobies in late winter-early spring prior to spawning to 10 000–15 000 gobies in late summer-early fall (Swift et al. 1989).

Population structure and lifespan

Population age structure, as revealed by the size distribution of fish collected by seine, was unimodal in most cases and changed most suddenly in spring or early summer (Swift et al. 1989, Worcester 1992, Swenson 1995). In most habitats around April or May, numbers of large adults decreased sharply while numbers of juveniles increased, resulting in a drop in mean size (Figure 2). These data indicate that the tidewater goby lives mostly one year only: by late spring the large adults had died after the spring spawning season, while juveniles spawned earlier in the season had grown large enough to be caught in the seine. In Pescadero marsh in 1992, however, the pattern was slightly different (Figure 3). Large adults did not disappear after the spring spawning season, but remained present in significant numbers for most of the year. Size distribution in the marsh was bimodal during the summer, indicating the persistence of adults and the recruitment of juveniles. In 1993, however, the pattern in Pescadero marsh was more similar to that seen at other sites.

Tidewater gobies generally live no more than a year in the wild, although fish in marsh habitats may

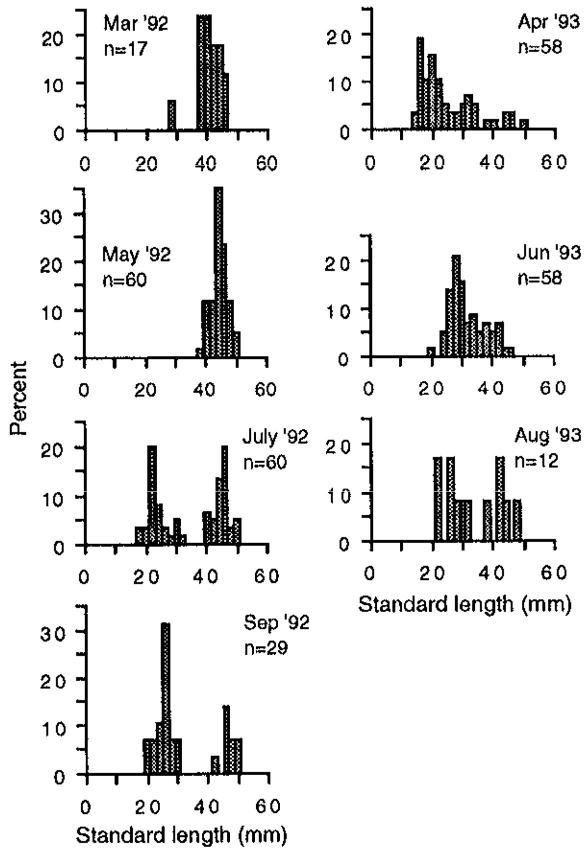

Figure 3. Size frequency distribution of tidewater gobies from Pescadero marsh, March 1992-August 1993. Adapted from Swenson (1995).

possibly live longer (Swenson 1995) and captive individuals can live up to three years (D. Vandenbergh-Wilson personal communication). Management of small short-lived species is inherently different from that of large longer-lived species because in small populations, short-lived species are typically more prone to extinction than long-lived species (Hendrickson & Books 1991). The tidewater goby's short lifespan increases its vulnerability to stochastic events. Disease, toxic pollution, adverse hydrological conditions (e.g., drought, floods, water diversion by humans), or poor recruitment in a single year have the potential to decimate a population due to the nearly complete turnover of individuals in a localized area. Almost continual monitoring is necessary because a population's status can change abruptly from abundant to rare or extirpated (Minckley et al. 1991).

This vulnerability is illustrated by the sudden disappearance of tidewater gobies in Pescadero (Swenson 1995). Gobies virtually disappeared from the lagoon from March 1992 to October 1993, and were rare in the creek from July 1992 to April 1993. Spawning occurred in the lagoon and creek in the summer and fall of 1991 and spring of 1992, but occurred only briefly in the creek in 1993 and not at all in the lagoon. Recruitment apparently failed, resulting in the loss of the lagoon and creek segments of the population once the adults died after spring 1992. Parasitism may have contributed to the decline. As discussed in a following section, tidewater gobies in the creek and lagoon were more heavily parasitized than gobies in the marsh. Toxic pollution may have also been a factor. Runoff from farms in the surrounding watershed can carry pesticide or herbicide residues. Fish kills have been documented in 1986 (Smith[2]) and 1995 in Butano Creek, a tributary than joins Pescadero Creek just above the lagoon. The dead and dying fish and invertebrates that resulted from the 1986 pesticide spill were quickly eliminated by piscivorous birds. Such events are thus difficult to detect, but their effects may extend well into the future if a significant portion of the fish population is affected.

Reproduction

Males dig and defend spawning burrows in soft sediment (Swift et al. 1989, Swenson 1997). The burrows are difficult to detect in the field, but tidewater gobies readily adopt polyvinyl chloride (PVC) tubes for spawning, both in captivity and in the field (R.N. Lea personal communication, Swenson 1997). I used tubes to collect and observe breeding fish, to quantify reproductive output, and to determine the timing and intensity of spawning activity (Swenson 1995). Short segments of PVC pipe (13 cm long, 1.27 cm inner diameter) were lined with a plastic sheet (to allow removal of egg clutches) and placed into the sediment for two weeks.

Sexual maturity is attained by males at 24 mm SL and by females at 27 mm SL (Swift et al. 1989, Swenson 1995). The mean size of spawning fish collected in tube traps at San Gregorio and Pescadero was 33 mm SL for males (SD = 5.7 mm, range 24–48 mm, n = 365) and 35 mm SL for females (SD = 4.9 mm, range 28–47 mm, n = 97).

Female fecundity (n = 22) was a linear function of length (mm) ($37.0 * SL - 691.9$, $r^2 = 0.61$, $p < 0.001$) and weight (g) ($598.9 * W + 102.0$, $r^2 = 0.77$, $p < 0.001$) (Swenson 1995). Ovaries contained 362–1010 mature ova (mean ± SD = 607 ± 206, n = 23). Clutches collected in tube traps contained approximately 100–1000 fertilized eggs (mean ± SD = 407 ± 179, n = 163), with the largest clutches coming from the marsh habitat at both San Gregorio and Pescadero. As discussed earlier, the largest fish were found in marsh habitats.

The tidewater goby's reproductive behavior is moderately sex-role reversed, with females exhibiting courtship behavior and more intense intrasexual aggression and breeding coloration than males (Swenson 1997). This is in contrast to other gobiid species (e.g., Tavolga 1954, Kinzer 1960, Brothers 1975). Observation of captive fish revealed that the female lays her entire clutch with a single male and the male accepts only one clutch per brooding cycle. Field collections of clutches have indicated that males may accept more than one clutch (Swift et al. 1989), but this is uncommon (2 out of 352 clutches, Swenson 1995). The male cares for the embryos for 9–11 days until hatching, rarely if ever emerging to feed (Swenson 1997). Clutches are laid approximately 2.5 cm below the entrance of the tube or burrow.

Tidewater gobies are repeat spawners, as indicated by histological examination of ovaries (Goldberg 1977) and observations of captive fish (Swenson 1995). Individuals of both sexes spawned 4–6 times in captivity, and one Pescadero female spawned twelve times. Clutch size varied unpredictably within females, as indicated by one 43 mm SL female that laid six clutches (mean ± SD = 839 ± 228 eggs, range 435–1063 eggs) over four months (6 January – 7 May 1992). Laboratory tests revealed that females can repeat spawn over shorter intervals (mean ± SE = 12.8 ± 0.9 d, range 9–24 d) than males (15.4 ± 0.9 d, 12–23 d) (Mann Whitney U, $p < 0.008$). This disparity in potential reproductive rate (Clutton-Brock & Vincent 1991) can produce a female-biased operational sex ratio, resulting in female-female competition for access to mates (Swenson 1995, 1997).

Tidewater gobies breed readily in captivity using PVC tubes (personal observation) or by burrowing into sand substrate (Swift et al. 1989, personal observation). When offered two different sediments, they preferred to spawn in sand rather than mud (Swenson unpublished data). This suggests that sandy lagoons may provide more favorable habitat for spawning than muddy habitats such as marshes or creeks. Captive fish spawned regularly at 8–15 ppt and 17–22°C (personal observation). Larvae and juveniles have been successfully raised to reproductive maturity on green algae, rotifers, and *Artemia* nauplii (D. Wilson-Vandenbergh & R. Lea personal communication). Captive breeding is a potential management tool for reintroduction or supplementation efforts, although the risk exists for loss of genetic diversity, artificial selection of inappropriate traits, and introduction of disease to the wild (Stewart 1991, Philippart 1995).

Spawning activity of wild fish was studied at San Gregorio and Pescadero by measuring the occupancy rate of tube traps (percent of tubes occupied by spawning pairs or males brooding clutches), which reflected the proportion of the population that was spawning (Swenson 1995). Spawning occurred over a wide range of salinities (2–27 ppt) and temperatures (9–25°C). Spawning occurred in all months except December, although the exact timing varied across years and among habitats. The peak in spawning activity occurred during the spring, as measured by the occupancy rate of tubes (Figure 4). Spawning activity declined in May and June, along with the number of large adults in the population as noted earlier (Figure 2). A second, smaller pulse of spawning activity occurred in late summer, by which time the cohort of the previous spawning period (late winter and spring of the same year) had reached sexual maturity. Fluctuations in reproduction were probably due to the death of breeding adults in early summer and colder temperatures or hydrological disruptions in winter (Swift et al. 1989). High temperatures, which can inhibit reproductive function (de Vlaming 1972), could have contributed to the mid-summer lull (e.g., Gill et al. 1996), although spawning usually resumed in

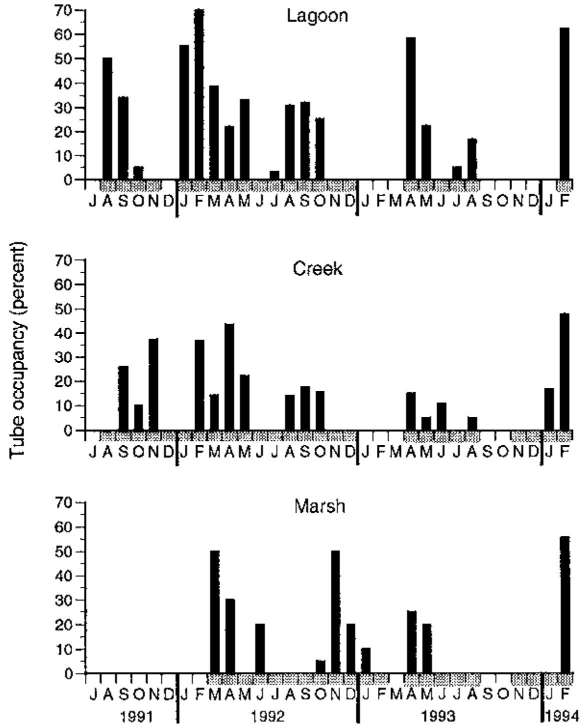

Figure 4. Spawning activity of tidewater gobies (percent of tube traps occupied by spawning pairs or brooding males) at San Gregorio, July 1991–February 1994. The shading along the horizontal axis indicates months when PVC tube traps were successfully retrieved. From Swenson (1995).

August and September when temperatures were still high.

Conclusions drawn from collection of spawning pairs and egg clutches (Swenson 1995) support other findings of spawning seasonality based on collections of young-of-the year fish from May to December (Swift et al. 1989, Worcester 1992). The capacity for year-round spawning is supported by ovarian histology. Females in pre-spawning condition (ovaries contained mature ova) made up 67-84% of females during March-June and 21–60% during July-February (Goldberg 1977). The prolonged spawning season observed in the field may reflect both extended breeding and variation in reproductive schedule among individuals.

Estimating the lifetime reproductive success (LRS) of the tidewater goby could be a useful parameter for conservation management. Because the tidewater goby essentially lives only one year, an estimate of annual reproductive output (number of embryos in a guarded clutch) is a good first approximation of LRS. Further refinement of this estimate would ultimately require determining hatching success, mortality rates of larvae, recruitment, and predation rates. The annual reproductive output can be roughly estimated based on data available on mean clutch size, spawning frequency and occurrence, lifespan, and length of breeding season. I assumed that a female can spawn three to six times in the wild during a spawning season (main peak in spring and a smaller, shorter pulse in late summer), a male can care for two clutches per month, and the average clutch size is 407 embryos (derived from counts of clutches guarded by males). The estimated annual reproductive output for a female that spawns in both spawning seasons (6–12 times in a lifetime) is approximately 2400–4800 embryos. A female that was produced during the late summer spawning season may not survive beyond the following spring spawning season and thus would produce an estimated 1200–2400 embryos.

The combination of iteroparity and prolonged spawning season suggests that a population could recover quickly if the physical conditions were suitable. Reintroduction to localities where tidewater gobies previously existed is a potential restoration tool. Efforts should be made to use fish from nearby populations as founder stock, however, to preserve metapopulation genetic structure. Two populations were reestablished in 1991 when tidewater gobies were translocated to Malibu Lagoon (52 fish) (Swift et al. 1993) and Waddell Creek lagoon (231 fish) (J. Smith personal communication) from nearby streams. By 1996 tidewater gobies were still present at Malibu Lagoon. They were also present at low numbers in Waddell Creek Lagoon, which had experienced some scouring after two high-flow winter rainy seasons (J. Smith personal communication).

Dispersal

Many estuarine (e.g., arrow goby and bay goby, Brothers 1975) and freshwater gobies (e.g., amphidromous Hawaiian gobies, Radtke et al. 1988) have pelagic larvae that disperse to other localities via the ocean. The tidewater goby, however, apparently spends its entire life in lagoons and the upper estuary (Swift et al. 1989). The duration of its pelagic larva period is unknown. The opportunity for interchange among populations or dispersal to new localities is therefore limited. Crabtree (1985) found genetic differentiation in allozymes among twelve populations, which suggests that gene flow is restricted.

Recolonization of extirpated populations is rare but possible (Swift et al. 1989, 1993). Although such occurrences could merely reflect more thorough sampling efforts, recolonization is a possibility in streams that have been previously well-sampled without success (Swift et al. 1993). Kevin Lafferty (unpublished) has proposed that during winters with extremely heavy rainfall, as seen in 1994–1995, the resulting floods sweep gobies into the Pacific Ocean, where the offshore current can carry then up to 9 km downcoast to other estuaries (downcoast is south for most of California and east along the Santa Barbara coastline). This suggests that populations at the northern ends of population clusters are more likely source populations than southern populations within the cluster. Swift et al. (1989) concluded that the potential for interchange and recolonization had declined as local extinctions reduced the number of source populations and increased their physical separation.

Diet and feeding behavior

The tidewater goby feeds primarily on crustaceans, dipteran larvae, gastropods and invertebrate eggs (Swift et al. 1989). Swenson & McCray (1996) studied seasonal and spatial variability in the diet of fish from three habitats (the lagoon and creek in San Gregorio and in the marsh at Pescadero) in three months. Tidewater gobies fed on benthic invertebrates, principally ostracods, chironomid larvae, and the amphipod *Corophium spinicorne*. The tidewater goby's diet was similar to but less diverse than the diets of other California estuarine gobies (Brothers 1975, Grossman et al. 1980) which occupy more marine habitats. Diet variability was low within each sample. However, when the diet and available prey were compared in August, different patterns of selectivity were revealed among gobies from the three habitats. Gobies consumed disproportionately more ostracods in the lagoon and more chironomid larvae in the marsh, but fed more generally in the creek. Thus, the tidewater goby appeared to be a specialist predator in certain habitats, but its preferences were not constant across habitats and it may forage opportunistically under some circumstances.

Observations of feeding behavior suggested that substrate differences among the habitats could result in habitat-specific foraging styles: sifting sand in the mouth, plucking prey from the substrate surface, and attacking prey in midwater. The sandy substrate of the lagoon would facilitate the sediment sifting method of feeding. Small meiofauna such as ostracods could be more easily obtained by filtering sand through the gill rakers. This method would be less successful in the creek, where small gravel is a dominant component of the substrate, or the marsh, where the fine mud is too light to settle out in the goby's mouth.

Swenson & McCray's (1996) study suggested that the tidewater goby's food requirements are adaptable to a variety of habitats, an advantageous trait in a fluctuating estuarine environment (Grossman et al. 1980). Overall invertebrate abundance in seasonally closed lagoons is suppressed following breaching of the sandbar at the mouth, due to the sudden change from low- to high-salinity conditions (Robinson 1993). Repeated disturbance from frequent breaching events could jeopardize food supplies for tidewater gobies in lagoon habitats. Marshes may provide better feeding opportunities, as suggested by the large size of gobies from these habitats, because the habitat conditions do not fluctuate as much.

Parasites

In 1991 and 1992, black spots were occasionally found on tidewater gobies in Pescadero lagoon and creek (Swenson 1995). These spots were cysts of the digenean trematode, possibly *Cryptocotyle lingua* (Swift et al. 1989), a widely distributed parasite in the northern hemisphere (Wood & Matthews 1987). *C. lingua* uses snails as the first intermediate host, various species of fishes as the second intermediate host, and piscivorous birds, such as gulls, as the definitive host (Stunkard 1930). The cercariae penetrate the skin of the fish, where they transform to metacercariae, become encysted, and are pigmented with melanin. Infection can kill the host fish, particularly juveniles, at high intensities (Sindermann & Rosenfield 1954, Sindermann 1966 , Lemly & Esch 1984), or facilitate secondary bacterial infections in the ruptured skin (McQueen et al. 1973). In addition to pathological impacts, parasite infection could increase the fish's vulnerability to predation, either by increased visibility due to the black cysts, or by altered predator-avoidance behavior (reviewed in Barnard & Behnke 1990).

Great numbers of small black snails, possibly *Assiminea californica* (Ricketts et al. 1985, Robinson 1993), were observed in Pescadero lagoon during 1991, but none in Pescadero marsh or at San Gregorio and none during 1992 (Swenson 1995). Many lagoon fish and some creek fish were heavily parasitized (> 100 metacercarial cysts), but infection was uncommon and at low levels in the marsh. Subsequently, tidewater gobies were scarce or absent in the lagoon and creek until spring 1993, when a few were found in the creek and lagoon. In 1993 infection was occasional and moderate (approximately 10–40 cysts) in the creek, and widespread and moderate in November 1994 in the marsh.

Introduced fishes

Moyle & Williams (1990) concluded that water diversions and introduced species, acting in concert, are the principal agents responsible for the decline of native fishes in California. Introduced predators such as green sunfish *Lepomis cyanellus*, smallmouth bass *Micropterus dolomieu*, and striped bass *Morone saxatilis*, may have contributed to the elimination of several tidewater goby populations (Swift et al. 1989). Potential predation and competition from introduced gobies, such as the yellowfin goby *Acanthogobius flavimanus*, chameleon goby *Tridentiger trigonocephalus*, and shimofuri goby *T.*

bifasciatus are also a concern (Wang[6], C. Swift personal communication, R. Swenson & S. Matern unpublished data). The tidewater goby may be more vulnerable to predation than other estuarine gobies in California because it only uses burrows for reproduction, whereas the arrow goby and bay goby use burrows for both reproduction and as shelter from predators and dessication (Brothers 1975, Grossman 1979). Introduced fishes can also disrupt feeding and courtship behavior, as observed in captive tidewater gobies held with shimofuri gobies (Swenson & Matern unpublished data).

Discussion

Consequences for conservation

The ecological and behavioral factors that make the tidewater goby a species at risk include its preference for stillwater and low-salinity habitats which are not abundant, isolation of populations, short lifespan, lack of marine dispersal, and vulnerability to introduced predatory fishes (Swift et al. 1989, Minckley & Deacon 1991, Lafferty et al. 1996). Its life history style of early sexual maturation, multiple spawnings, almost complete annual turnover in population structure, and short lifespan probably evolved in response to unpredictable adult mortality, such as from predation or environmental disturbance (Miller 1984, 1990). Attributes that favor the tidewater goby's recovery include euryhaline tolerances, rapid reproductive rate, potential for opportunistic feeding, the possibility of natural recolonization in some instances, and the success of captive breeding and limited reintroduction efforts.

The tidewater goby shares certain attributes with other species that are vulnerable to extinction. In California's native fish fauna, Moyle & Williams (1990) found that threatened taxa tend to be endemic to California, restricted to a small area that may involve only a single drainage basin, and part of a fish community of fewer than five species. Miller (1990) identified traits in endangered Mediterranean freshwater gobies, such as restriction to relatively confined habitats, small size and cryptobenthic behavior that may reduce vagility, and lack of recolonization among isolated drainages via estuaries or coastal waters due to their freshwater habitat requirements. These Mediterranean gobies may be close ecological correlates of the tidewater goby (Swift et al. 1989). In discussing the conservation and management of cyprinodontids in western America, Minckley et al. (1991) noted that these fishes are evolutionarily inexperienced with aggressive predators and are short-lived.

In light of its natural history and behavior, several measures could be implemented to conserve tidewater goby populations. Habitat protection and restoration are critical (Moyle & Williams 1990, Moyle 1995, Capelli 1997). Measures for the tidewater goby include protecting coastal marshes that adjoin creeks and lagoons, maintaining natural flow regimes, preventing artificial breaching of creek mouths (especially during the summer and fall when there is little freshwater inflow), and preventing introductions of predatory fishes.

Translocation and captive breeding (in conjunction with reintroduction to the wild) can be potential tools for recovery, provided certain criteria are met. Major considerations for translocations include the availability, suitability, and security of habitat at a reintroduction site; potential effects of obtaining parent stock on the donor population; genetic integrity of the transplanted individuals; and avoiding transfer of diseases or parasites (reviewed by Hendrickson & Brooks 1991, Stewart 1991, Maitland 1995, Minckley 1995). Captive breeding with reintroduction should be considered a temporary measure to reestablish self-sustaining populations, because of the risks of diminished genetic variability and unintentional selection for ill-adapted genotypes (Philippart 1995). Individuals for translocation or captive breeding ideally should be obtained from the population closest to the target site, given the tidewater goby's discontinuous distribution along the coast and the isolation among populations. All reintroduced populations should be mon-

[6] Wang, J.C.S. 1982. Early life history and protection of the tidewater goby *Eucyclogobius newberryi* (Girard) in the Rodeo Lagoon of the Golden Gate National Recreation Area. Tech. Report No. 7, Cooperative National Park Resources Studies Unit, University of California at Davis. 24 pp.

itored, at least annually for this short-lived species, to determine population survival and establishment, evaluate population growth, and provide opportunities for research on translocation as a conservation tool (Minckley 1995, Rakes et al. 1999 this issue).

Additional research into the tidewater goby's utilization of marsh habitats, dispersal mechanisms, and response to artificial breaching events would provide additional information for management. Further genetic studies to examine metapopulation structure would indicate the degree of isolation among populations and guide selection of populations both for designation of preserves and for use as brood stock in potential translocation efforts. The U.S. Fish & Wildlife Service is currently preparing a recovery plan which will identify critical habitat and make recommendations for the protection and restoration of the tidewater goby.

Applications of behavior to fish conservation

Behavioral studies are often overlooked as a tool for management of endangered fishes, as management has emphasized distribution and life history (Francis-Floyd & Williams 1995). But as illustrated above by the tidewater goby, understanding the behavioral aspects of natural history can be useful for the management of fishes (reviewed by O'Hara 1993, Barlow 1995) and other species at risk of extinction (e.g., Walters 1991, Greene 1994). For example, population differences can be detected on the basis of behavior, such as differences in the timing of spawning migrations within salmon species (Groot & Margolis 1991), which can lead to protection of unique population segments. Distinct stocks of salmonids are now being managed by the National Marine Fisheries Service as Evolutionarily Significant Units (ESUs) under the Endangered Species Act (Waples 1991, 1995). In toxicology studies, identification of exposure pathways can depend on understanding feeding and reproductive behavior. For example, the burrowing behavior of tidewater gobies can increase exposure of males and developing eggs to sediment-borne toxins.

The design and utilization of sampling gear can be improved by understanding life history and behavior, as illustrated by recent developments in commercial fisheries operations (Parrish 1999 this issue). In the case of the tidewater goby, tube trapping has been adopted by the U.S. Fish and Wildlife Service as an alternative sampling method. This method is not as effective or efficient as seining when conducting surveys to determine whether the species is present because tubes do not sample nonbreeding fish and are labor- and time-intensive. This example points out the potential pitfalls involved when applying methods and theories of population and behavioral ecology to conservation and management problems (Simberloff 1988, Walters 1991).

Understanding habitat preferences can guide habitat restoration (e.g., artificial reefs, Bohnsack 1989), reintroduction programs (Hendrickson & Brooks 1991), and designation of critical habitat for protection. The rheotropic responses of migrating salmonids have been utilized in the design of fish ladders over dams and other barriers (O'Hara 1993). Behavioral studies can also enhance captive breeding programs (Francis-Floyd & Williams 1995). By studying behavior we learn how organisms are adapted to their environments and thus can better develop strategies for protection and enhancement (Barlow 1995).

Acknowledgements

I wish to thank Camm Swift for sharing his vast knowledge of the tidewater goby, George Barlow for encouraging my research, Jerry Smith for introducing me to the San Gregorio and Pescadero ecosystems, Tom Taylor and Mark Capelli for their constructive comments on the manuscript, and the California Department of Parks and Recreation for permitting me to conduct research at these state parks. This paper benefitted from the reviews by Gene Helfman, C. Swift, and two anonymous reviewers. My doctoral research was supported by fellowships from the National Science Foundation (Predoctoral Fellowship), the University of California at Berkeley, and the Association for Women in Science. Research funds were provided by the

American Society of Ichthyologists and Herpetologists (Rancy Award), the American Museum of Natural History (Lerner Gray Award), Sigma Xi, the Museum of Vertebrate Zoology (Wilhelm L. F. Martens Fund), and Department of Integrative Biology of the University of California at Berkeley. Travel support was provided by Trihey & Associates, Inc.

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